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***** Accepted manuscript published in** *Journal of Archaeological Science* **39, 7 (2012) 2023-2035 (**http://dx.doi.org/10.1016/j.jas.2012.04.004**) *****

Seasonality of birth and diet of pigs from stable isotope analyses of tooth enamel ($\delta^{18}O$, $\delta^{13}C$): a modern reference data set from Corsica, France

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Abstract

Since domestication during the mid 11th millennium BP in the Near East and the 8th millennium BP in China, the pig has played an important role in human diet and economy. The objective of this study is to evaluate the potential of stable oxygen and carbon isotopes sequential analyses of pig tooth enamel to investigate pig seasonality of birth and diet, as these are important parameters for the reconstruction of pig herding strategies in ancient societies.

A pilot study was performed on a modern reference set composed of five free-range Corsican domestic pigs and four Corsican feral pigs. Tooth enamel from the mandibular incisors (I_1, I_2), molars (M_2, M_3) and canines (C) were sampled sequentially to map the stable oxygen and carbon isotope records in the pig mandible.

The sequences of $\delta^{18}O$ published in this paper may be used as a reference data set for births grouped in mid-autumn and late winter. The $\delta^{13}C$ values measured in the wild pigs constitute the first reference set for a wild population living in a Mediterranean environment. Results show that among all sampled teeth (I_1, I_2, C, M_1 and M_2), the combination of the sequences of $\delta^{18}O$ measured in the first and second incisors provides the most effective data for determination of birth seasonality. The sequences of $\delta^{18}O$ measured in the second and third molars were too short and/or dampened to be interpreted in terms of seasonality. In domestic pigs, male evergrowing canines provide a one and a half year record, allowing observation of short-term seasonal variations in the isotopic composition of diet.

Applied to archaeological assemblages, the joint stable isotope analysis of incisors and canines will enable the qualification of the seasonal rhythm of pig herding practices, including slaughtering strategies, in more concrete terms. These practices are directly linked to the modalities of pork production but also to the availability of food resources.

Keywords: Pig; Tooth enamel; Stable oxygen and carbon isotopes; Birth and diet seasonality; Sequential sampling; Corsica.

Introduction

Since the first study by Koch et al. (1989), investigation of the stable isotopic record in dental tissues through serial sampling has been widely developed. Tooth enamel is preferentially sampled for sequential analysis of bioapatite, as attempted for the first time by Fricke and O'Neil (1996). In spite of methodological issues due to the complexity of the process of enamel deposition and mineralization (Balasse, 2002, 2003; Balasse et al., 2011; Fricke et al., 1998a; Blaise et Balasse, 2011; Hoppe et al., 2004; Passey and Cerling, 2002, 2004; Passey et al., 2005; Zazzo et al., 2005, 2010, 2012), it has since been widely applied to modern and archaeological specimens including low and high crowned teeth, as well as evergrowing teeth, to investigate paleoecology and paleoclimatology (Bernard et al., 2009; van Dam and Reichart, 2009; Botha et al., 2005; Fox and Fisher, 2001; Fricke et al., 1998b; Fraser et al., 2008; Nelson, 2005; Sharp and Cerling, 1998; Stuart-Williams and Schwarcz, 1997; Zazzo et al., 2002), seasonal mobility of wild and domestic herds and associated human mobility (Balasse and Ambrose, 2005; Balasse et al., 2002; Bentley and Knipper, 2005; Britton et al., 2009, 2011; Copeland et al., 2008; Henton et al., 2010; Pellegrini et al., 2008), diet (Balasse et al., 2005; 2006 and 2009; Copeland et al., 2009; Cerling et al., 2008; Feranec et al., 2009) and birth seasonality (Balasse and Tresset, 2007; Balasse et al., 2003; Blaise and Balasse, 2011; Henton et al., 2010; Stevens et al., 2011; Towers et al., 2011). This procedure has not been adapted to swine bunodont molar teeth or incisors. To date only a single study has been published using pig canines to investigate paleoclimates (Fricke et al., 1998a).

Despite the lack of research in this area, wild and domestic swine have been playing an important role in human diet and economy for millennia (Albarella et al., 2007; Lion and Michel; 2006; Nelson, 1998). Domestic pigs have been raised for meat, and perhaps fat, since the middle of the 11th millennium BP in the Near East (Vigne, 2011), and ca. 8th millenium BP in China (Cucchi et al., 2011). Local domestications in Europe are also suggested to have occurred ca. 7-5th millennia BP (Larson et al., 2007). The success of the pig as a domesticate may be partly ascribed to its prolificacy and ability to digest a wide range of food. Wild and domestic pigs may farrow once or twice a year depending on food availability (Etienne, 2003), and because they can eat almost everything, they can be found at any step in the food web, from strict herbivory to nearly carnivory (Albarella et al., 2006). This plasticity in reproductive and dietary behaviours was most probably exploited by ancient pastoral communities, but has been difficult to assess *a priori* in archaeological assemblages.

Stable isotope studies have been performed on pig archaeological remains. They consist mainly of stable carbon and nitrogen isotope analysis of bone collagen, carried out to investigate management of domestic pig diet, contribution of pig meat to human diet and more widely the structure of food webs and the ecology of past and current wild boar populations (Bocherens et al., 1991; Bösl et al., 2006; Ervynck et al., 2007; Hamilton et al., 2009; Müldner and Richards, 2005; Mulville et al., 2009; Richards et al., 2002; Rosvold et al., 2010). Some analyses were also performed on bulk enamel bioapatite from modern specimens for a more precise definition of the isotope enrichments occurring from diet to bone tissues (Passey et al., 2005b; Warinner and Tuross, 2009). These studies, involving bone or bulk tooth enamel, investigate diet at yearly to multi-annual scales.

Pig birth seasonality is also investigated using other approaches including detailed recording of tooth eruption and attrition (Ervynck, 2005; Horard-Herbin, 1997; Oueslati, 2002), and the study of enamel linear hypoplasia (Clavel and Sicard, 2007; Dobney and Ervynck; 2000; Ervynck and Dobney, 2002). However, these techniques are indirect means of studying birth patterns. As a result, it is difficult to assess birth seasonality with certainty using such approaches.

In order to investigate pig annual birth distribution and dietary behaviour at a seasonal scale, we performed a pilot study on a modern reference set of wild and free-range domestic pigs from Corsica (France). This survey will provide us with a reference data set to investigate birth seasonality and feeding behaviour of pigs in archaeological contexts. This pilot study compared the $\delta^{18}O$ and $\delta^{13}C$ records through sequential sampling of tooth enamel on incisors, molars and canines to assess whether a seasonal signal is identifiable, and to define the most appropriate sampling protocol for future studies. The variation in C and O stable isotope ratios was then compared in domestic and wild populations to investigate whether differences in the record of the seasonal variations of the diet could be identified between wild and domestic pigs.

Material and Methods

2.1 The modern reference set

2.1.1 Environmental conditions

The modern reference set comes from Corsica (Fig.1), where altitude, relief and winds are responsible for wide diversity in climate and vegetation. The highest temperatures are registered in July and August and the lowest in January, more rarely in February. The wild and free ranging pigs in our reference set occupied biotopes spreading over four vegetation levels (Gauthier, 2002):

- the mesomediterranean level (600 – 900 m), covered by a dense maquis; evergreen holm oaks (*Quercus ilex*), Cork oaks (*Quercus suber*), pinaster (*Pinus pinaster*) forests, and short-grass prairies in its inferior horizon. Deciduous trees, including Durmast oak (*Quercus pubescens*) and chestnut tree (*Castanea sativa*), are present in the superior horizon;
- the supramediterranean level (500 to 1350 m), dominated by deciduous tree (*Quercus sp, Satanea sativa, Fagus sylvatica*). Evergreen trees and macchia still occur;
- the mountainous level (approximately 1000 m to 1800 m), characterized by the European silver fir (*Abies alba*) and beech. Mean annual temperatures are between 7 and 10°C, and a dry season lasts from mid-July to mid-August;
- the subalpine level (from 1400/1600 m to 2100 m) on the north-facing slopes, characterized by a widespread and very dense compound vegetation with an endemic alder (*Alnus viridis* subsp. *suaveolens*). Mean annual temperatures are between 3 and 7°C, and snow falls from November to May.

2.1.2 Corsican domestic pigs of Radicci

The domestic reference set is composed of five pigs (“Nustrale” breed, with rare occurrence of cross-breeding) from Radicci, southern Corsica (Fig.1), all coming from one farm. They were born in November 2006 and slaughtered between January and February 2009. All were castrated males. Usually castration occurs just after weaning, at the age of approximately two and a half months. They were reared in controlled free-range farming conditions (as defined in Lambert-Derkimba, 2007). The piglets were kept in enclosure for two months after birth. Later they were left to forage freely on surrounding pastures and holm oak forests, between 500 and 1000 m of altitude. They had access to water from streams and come back to the pigsty at night, where they were fed with pellets and watered from a running stream. Maize was also observed on the ground, suggesting that pigs were also fed this. From June of their second year, or September if there was enough food in the oak forest over the

summer, pigs were kept in an enclosure and fattened with pellets, though they seemed to prefer wheat and barley. Maize was not provided during the fattening period. In this area, oak acorns were the basis of the fattening diet.

We investigated the isotopic signature of the two main components of the pig diet using samples of the pellets especially designed for the Corsican breed by the French Institute for Agronomic Research (INRA) and samples of oak acorns and cups. Pellets were composed of barley (50 %), pea (15 %), middling (15 %), wheat (13 %) and sugar cane molasses. Evergreen holm oak acorns and cups were collected in the beginning of March 2009, in the forest surrounding Corte (Northern Corsica).

2.1.3 Corsican feral pigs

Corsican wild pigs are feral descendants of domestic pigs introduced to Corsica by early Neolithic people during the 6^{th} millennium BC (Poplin, 1979; Vigne, 1988). Although smaller than continental wild boars, Corsican feral pigs display all the behavioural and morphological traits of a wild population, but have retained their domestic heritage in their number of chromosomes (Popescu et al., 1980) and mtDNA (Larson et al., 2007). Four specimens were collected in different regions of Corsica (Fig.1 and Tab.1). Two were captured during the hunting season at Bocca di Pigna. The INRA of Corte collected the others during a trichinellosis survey campaign (2007-2008). Franceschi (1984) reported that wild pigs are encountered from the coastal region to high mountains. Wild boar lives preferentially in areas with the most abundant or favoured food and under dense canopy. During the warm season, they move up to the subalpine level, where they live preferentially under the tree cover of *Alnus viridis* subsp. *suaveolans* (Noblet, 1987). They move down when snow falls. The mating period stretches from the beginning of October to the beginning of January and depends on food availability, especially the abundance of acorns (Fonseca et al., 2004; Maillard and Fournier, 2004). Farrowing occurs from the end of January to the end of April (Noblet, 1987) with a peak from the end of February to mid-March (O. Maestrini, pers. com. 2011). They forage for food during the night and can cover great distances (Noblet, 1987). Seasonally, their diet can consists of cultivars and wild foods, including almonds, figs, grapes, walnuts, hazelnuts, sweet chesnuts or beechnuts. When these resources are not available, they can also eat berries, root crops especially of ferns, tubers and grass in spring. Five to ten percent of their diet is composed of animals: frogs, rodents, snakes, broods, fish, shellfish, snails and insect larvae (Baubet et al., 2008; Bouldoire and Vassant, 1989; Herrero et al., 2004; Noblet, 1987).

2.2 Principles of stable C and O isotope studies

The phosphate and carbonate oxygen in mammalian bioapatite precipitates in isotopic equilibrium with body water (Iacumin et al., 1996; Longinelli, 1984; Luz et al., 1984). The oxygen isotopic composition of body fluids reflects that of ingested water, including drinking water and water from plants. They both track the oxygen isotopic composition of meteoric water, which varies seasonally with ambient temperature at middle and high altitudes (Flanagan and Ehleringer, 1991; Land et al., 1980; Longinelli, 1984; Luz et al., 1984). The highest $\delta^{18}O$ values are recorded in the warmest months, the lowest in the coldest months (Dansgaard, 1964; Gat, 1980).

The stable carbon isotope ratio ($\delta^{13}C$) of bioapatite carbonates is a function of the $\delta^{13}C$ of bulk diet (Ambrose and Norr, 1993; Tieszen and Fagre, 1993). In terrestrial ecosystems, the main factor influencing the $\delta^{13}C$ of plants is their photosynthetic pathway. The modal value for C_3 and C_4 plants is -27 ‰ and -12 ‰ respectively (Tieszen and Boutton, 1989). The ^{13}C-

enrichment (ε*, as defined in Passey *et al.*, 2005b) between enamel bioapatite and diet was estimated as + 13.3 ‰ in pigs fed C_3 diet, with a mean difference of minus one per mil in pigs fed C_4 diet (Passey et al., 2005). Warinner and Tuross (2009) calculated a $\delta^{13}C$ spacing (Δ, as defined in Passey *et al.*, 2005b) of + 14.1 ‰ and + 14.3 ‰ in pigs raised on two mixed C_4/C_3 plant regimes. From their results, it is possible to infer the isotope enrichment (ε*) between porcine enamel and diet of + 14.4 ‰ and + 14.6 ‰ respectively. In Corsica, C_4 species represent at the most 6 % of vascular species, of which less than 60 % are native (Pyankov et al., 2010). Other factors may influence plant $\delta^{13}C$, including plant growth stage, time of day, season, aridity, salinity, luminosity and recycling of atmospheric CO_2 (Garten and Taylor, 1992; Gleixner et al., 1993; Heaton, 1999; Lowdon and Dick, 1974, Matus et al., 1995, Saranga et al., 1999).

Enamel forms by accretion and, once fully mineralized, is not remodelled. Therefore the sequence of isotopic variations preserved along the crown height constitutes a record of individual history over tooth growth. By performing sequential sampling perpendicularly to the tooth growth axis from the crown apex to the Enamel-Root Junction (hereafter referred to as ERJ), it is possible to measure a chronological sequence of $\delta^{18}O$ and $\delta^{13}C$ variations, providing new insights into seasonal changes in diet $\delta^{13}C$ and seasonality of birth (Fricke and O'Neil, 1996 and subsequent works). As timing of tooth development is fixed within a species, the same pattern of $\delta^{18}O$ variations is recorded at the same height of the tooth crown in individuals born at the same time of the year. The comparison of inter-individual variations of the $\delta^{18}O$ pattern for the same tooth may allow the distinction of different groups of birth (Balasse and Tresset, 2007; Balasse et al., 2003; Blaise and Balasse, 2011; Henton et al., 2010; Zazzo et al., 2002).

2.3 Timing of tooth formation in pigs

Although many references on mandibular teeth eruption exist (*e.g.* Anezaki, 2009; Bridault et al., 2000; Bull and Payne, 1982; Carter and Magnell, 2007; Hayashi et al., 1977; Magnell, 2002; McCance et al., 1961), only a few of them give information on crown formation time (Carter & Magnell, 2007; McCance et al., 1961; Robinson et al., 1987). Crown formation of the lower first incisor (I1) begins between one and three months-after birth and might carry on until 17 months (Fig.2). The crown of the lower second incisor (I2) begins to form from six to ten months after birth and possibly ends around 24 months-old. However, for these incisors, the only data available for the end of crown formation were eruption dates, and in some cases, gingival emergence dates. It is therefore most likely that the crown formation of these teeth ended several months before the age given in literature. Crown formation of the lower second molar (M2) is initiated from birth at the earliest and finishes eleven months after birth at the latest. The crown of the lower third molar (M3) begins to form from two months after birth at the earliest and can go on until 18 months. Finally, pig canines are sexual dimorphic (Bouldoire and Vassant, 1989). Female lower canines are small rooted teeth and the crown forms from birth at the earliest to 12 months at the latest. Male lower canines are evergrowing teeth and crown formation begins at the same time as with females but never stops until the death of the animal. These teeth, except potentially the apex of the canine and second molar, develop after weaning (Magnell and Carter, 2007; McCance et al., 1961), which is completed at the age of two months and a half in domestic pigs from Radicci. Wild piglets begin to eat solid foods after two weeks and are fully weaned after three to four months (Etienne, 2003).

2.4 Protocol

All the mandibles were firstly boiled in a saline aqueous solution to remove the remaining putrid flesh and start the degreasing of bones. After rinsing, they were boiled in a sodium perborate (NaBo3) solution and soap for bleaching and degreasing and then cooled at room temperature. The dried mandibles were finally plunged into a cologne spirits bath. The cologne spirits were changed until fat desaturation, to achieve degreasing.

Sequential sampling of tooth enamel previously conducted on pig lower second molars from the Neolithic site of Bercy (France) demonstrated that intra-tooth variations in $\delta^{18}O$ and $\delta^{13}C$ were difficult to interpret, possibly because of the shortness of the temporal sequence (Frémondeau, 2007). For this reason, it was decided to sample the lower third molar, as its crown development spans a longer time than in the lower second molar, the high crowned lower first and second incisors and the lower canine. Incisors and canines were extracted from the mandibles, brushed under warm water with soap and dried at room temperature. Molars were sampled while still attached in the mandibles. They were brushed and cleaned with dental tools.

Sampling of enamel powder was performed using a diamond drill bit (Fig.3). Each sample included the whole thickness of the enamel layer, from the apex to the ERJ of the crown, perpendicularly to the tooth growth axis. One-millimetre wide grooves were drilled on male canines, 0.5 mm grooves were drilled on the incisors, molars and female canines. The sampling spans the full width of the tooth lobe or crown. Molars were sampled on the lingual side on the anterior lobe. Incisors and canines were sampled on the labial side.

Enamel pre-treatment described in Balasse *et al.* (2002) was initially applied to 27 samples (REF PCR1 I2). Enamel powder was treated with sodium hypochlorite 2-3 % (0.1 ml solution/mg sample) for 24 hours to remove organic matter, rinsed five times with distilled water, and reacted with 0.1 M acetic acid (0.1 ml solution/mg sample) for 4 hours to remove diagenetic carbonates. It was rinsed five times again with distilled water and freeze-dried. This pre-treatment resulted in a constant shift (+1.5 ± 0.2 ‰) in $\delta^{18}O$ and in $\delta^{13}C$ values (+0.7 ± 0.2 ‰). Therefore, it was decided not to apply it to the remaining samples, because it induced an important weight loss (45 %). The values of REF PCR1 I2 presented here are those of the non pre-treated samples.

Bioapatite samples weighing around 600 µg were reacted with 100% phosphoric acid at 70°C in individual vessels in an automated cryogenic distillation system (Kiel IV device), interfaced with a Delta V Advantage isotope ratio mass spectrometer. Over the period of analysis of the bioapatite samples, the analytical precision estimated from 286 samples of the laboratory internal carbonate standard (Marbre LM, normalised to the NBS 19 international standard) was 0.02 ‰ for $\delta^{13}C$ and 0.08 ‰ for $\delta^{18}O$.

The acorns, still attached to their cups, were dried in an oven at approximately 60°C for eight days, freeze-dried for three hours and crushed to fine powder. The isotopic analyses were performed on acorns attached to their cups and on the cups and the different parts of the fruit (pericarp and seed) separately. The pellets were freeze-dried for three hours and crushed. The isotope values were measured using a Flash 2000 elemental analyser interfaced to a Delta V Advantage mass spectrometer. Over the sample run, the $\delta^{13}C$ analysis of six samples of caffeine (IAEA-600) produced the analytical precision of 0.32 ‰.

Results

3.1 Carbon isotope ratios of food samples

Carbon content and $\delta^{13}C$ of the food samples are presented in table 2. On average, the $\delta^{13}C$ values measured in acorns and cups vary from -26.7 ‰ to -25.5 ‰, according to the part of the item analysed. The highest value was always obtained from the seed, which was 0.8 to 1.2 ‰ ^{13}C-enriched compared to the pericarp and the cup. These values are within the typical range of C_3 plant $\delta^{13}C$ values (-34 ‰ to -22 ‰), and slightly higher than the modal value of -27 ‰ reported for terrestrial C_3 plants from temperate environments (Heaton, 1999; O'Leary, 1988; Tieszen, 1991; Tieszen and Boutton, 1989). Leaf $\delta^{13}C$ values measured in *Quercus ilex* from Mediterranean ecosystems in southern France range from -29.1 to -24.7 ‰, with a mean value of -27.4 ‰ (Damesin et al. 1997). Higher $\delta^{13}C$ values in acorn might be explained by the high carbohydrate content of the seed (Heaton, 1999). Moreover, acorns are ripe by September or October, after a six-month development. Consequently, acorns ripen during the warmest and most arid months of the year, when $\delta^{13}C$ is the highest (e.g. Heaton 1999; Tieszen 1991; Tieszen et Boutton 1989). Another explanation could be the differential use of diurnal ^{13}C-depleted versus nocturnal ^{13}C-enriched sucrose between leaves and non-photosynthetic tissues like fruits (Cernusak et al., 2009). The $\delta^{13}C$ mean value measured in pellets was -27.2 ‰, showing no significant contribution of sugar cane molasses (C_4).

3.2 Carbon and oxygen isotope ratios in domestic pigs

Results are presented in figure 4 and table 3. The $\delta^{18}O$ values measured in domestic pigs ranged from -6.2 ‰ to -3.6 ‰. When the optima were identifiable, the amplitude of variation averaged 1.4 ‰ in I2, 1.9 ‰ in canines and 0.9 ‰ in M3. The sequence measured in male canines over approximately 100 mm spanned roughly a year and a half. In the other teeth, the annual cycle was only partly recorded. In the I1, the highest $\delta^{18}O$ values were recorded between 15 and 25 mm from the ERJ. In the I2, the lowest $\delta^{18}O$ values were recorded from 23 to 35 mm from the ERJ. In the M3, the lowest $\delta^{18}O$ values were recorded between 3.8 and 5 mm.

$\delta^{13}C$ values ranged from -14.0 ‰ to -5.5 ‰. Over a sequence representing slightly more than whole annual cycle the amplitude of variation averaged 5.3 ‰ in canines.

3.3 Carbon and oxygen isotope ratios in feral pigs

Results are presented in figure 5 and table 4. The $\delta^{18}O$ values measured from feral pigs ranged from -7.3 ‰ to -2.6 ‰. The amplitude of variation averaged 2.8 ‰ in canines, where a sequence spanning almost two annual cycles was measured over 100 mm. In the I1, the lowest $\delta^{18}O$ values were recorded between 14 and 21 mm from the ERJ. In the I2, the highest $\delta^{18}O$ values were recorded at around 17 mm from the ERJ in SC3 and SC4 and around 8 mm from the ERJ of SC1 and SC2. In the M3, the lowest $\delta^{18}O$ values were recorded between 4 mm (SC1) and 7 mm (SC2 and SC4) from the ERJ. A minimum $\delta^{18}O$ value was noted between approximately 17 and 20 mm from the ERJ of the female canine.

$\delta^{13}C$ values ranged from -16.8 ‰ to -12.1 ‰. The amplitude of variation averaged 1.9‰ in canines, with cyclical variations following roughly those measured in the $\delta^{18}O$.

Discussion

4.1 Chronology of tooth development in *suidae*

Tooth enamel mineralization is a two-stage process beginning with the secretion of a poorly mineralized matrix (~30 % mineral per volume; Kirkham et al., 1988), followed by the replacement of most of the organic matrix by mineral during maturation (Suga, 1982; Suga and Gustafson, 1963; Suga et al., 1970; Weinmann et al., 1942). In the present study, $\delta^{18}O$ sequences were obtained from the analysis of carbonate, whose timing and rate of incorporation in developing enamel is not precisely known. The comparison between the timing of tooth development and $\delta^{18}O$ sequences could give information on the delay between tooth formation and isotope profiles. This delay was demonstrated to be mostly due to the time required for enamel to achieve mineralization, even though it is also influenced by the turnover time of oxygen and carbon in the body fluids (Ayliffe et al., 2004; Podlesak et al., 2008, Zazzo et al., 2010).

The variations recorded in enamel most likely reflect the annual seasonal cycle. Figure 2 compares the timing of tooth formation in pigs born in November with the stable oxygen isotope record in tooth enamel carbonate, from which the season of mineralization was inferred. In these 26 month-old domestic pigs, the stable oxygen isotope record in the enamel carbonate spans:

- the last two thirds to three quarters of the first year in I1 (in this tooth, approximately 2 to 3 mm of the crown were lost by attrition);
- the end of the first year to the first two thirds of the second year in I2;
- only a few months towards the middle of the first year in M2 (missing 3 to 4 mm by attrition);
- the middle of the first year to the middle of the second year in the M3;
- the whole life from the second half of the first year in male canines.

This timing of mineralization fits within the timing for tooth formation given by literature, with a likely slight delay for completion of mineralization, as highlighted by the fact that the stable oxygen isotope record of the unworn teeth starts after the later estimation for the beginning of tooth crown formation (Fig.2). It was not possible to estimate more precisely this delay, as no data was available on tooth crown formation in the analyzed breed. The Corsican breed is characterized by slow maturation and it is likely that tooth formation timing would be closer to the later estimations reported in Figure 2, leading to a duration of only a few months for enamel mineralization. However, it is not possible to hold this theory as a firm conclusion.

In this regard, at the individual scale, different teeth with overlapping mineralization timing did not provide the same optima values. For example, higher $\delta^{13}C$ maxima were measured in the canine than in the I2, in spite of a higher sampling resolution in I2 (Fig.3). This suggests that the dampening of the isotopic signal is different according to the tooth, which can be explained by a difference in the carbonate accumulation rate. Indeed, incisors record half an annual cycle over approximately 20 to 25 mm, M3 over roughly 6 mm, and male canines over approximately 25 to 30 mm (Fig.4). Therefore the rate of accumulation of carbonate appears to be slower in the M3 than in the incisors and canine. Both incisors seem to have the same carbonate accumulation rate. A faster carbonate accumulation rate was observed for male evergrowing canines, which are consequently characterized by the less dampened amplitude of variation in stable isotope ratios, despite the use of a diamond drill bit of bigger diameter than for the other sampled teeth. This was expected from a considerably thinner enamel layer in the male canines compared to other teeth.

4.2 Assessing birth seasonality

4.2.1 Choice of the tooth

The male canines provided the longest time sequences, spanning approximately a year and a half over 100 mm in these 26 month-old pigs and almost two years in SC4 over the same length. The seasonal cycle was clearly identified from this tooth. However, because male canines are evergrowing teeth, the sequence recorded from this tooth could not be compared between individuals with different ages because of the lack of a reference point (ERJ in other teeth) used to relate the sequence to a developmental stage of the tooth. Concerning the M2, even with minimal wear (e.g. SC3 M2), the identification of the part of the seasonal cycle represented by the $\delta^{18}O$ sequences and assessment of the shift between individuals remained difficult. Similarly, due to the dampening of the isotopic signal, interpreting precise inter-variability from M3 sequences was difficult. As the isotopic signal was less dampened in incisors than in molars, these teeth provided more easily readable sequences. Their crown development timing and $\delta^{18}O$ values also overlapped. It was therefore possible to match the two incisors curves in one sequence, in order to obtain a sequence over a whole seasonal cycle (Fig.6a and 7a). The matching was performed graphically. The correction applied was achieved by setting the ERJ of I1 at 27 mm from the ERJ of I2 (Fig.6 and 7). This correction corresponded approximately to the median value for the best fit in all individuals. Therefore, incisors appeared to be the most suitable teeth for the study of birth seasonality. Consequently, the following discussion will concentrate on these teeth.

4.2.2 Inter-individual variability in the $\delta^{18}O$ values

In the incisors of the Radicci domestic pigs, inter-individual variability in the record of $\delta^{18}O$ (*i.e.* location in tooth crown of the maxima and minima) is approximately 5 mm for I1 and 12 mm for I2. This might be partly due to the variability of the date of birth – all pigs were born in November, but with unknown dates of birth – and / or variability in the timing of growth and of tooth size. Tooth size can be accounted for by normalizing the distances from ERJ to a mean crown height for all individuals. The first incisors were too worn for their initial crown height to be estimated. Consequently, normalization could not be performed on this tooth. The crown height of the I2 varied between 37.6 and 43.0 mm. When distances from the ERJ were normalized to a mean crown height (40.2 mm), inter-individual variability in the record of $\delta^{18}O$ along tooth crown was reduced to approximately 8 mm (Fig.8).

In the four feral pigs, the inter-individual variability in the location of the minima and maxima was approximately 6 mm in I1 and 10 mm in I2. This was very similar to what was observed in the incisors of domestic pigs for births grouped in one month. This suggests grouped births (Fig.5 & 7a). Noblet (1987) reported that farrowing among Corsican wild pigs occurs over a short period of three months from the end of January to the end of April. However a peak of births is observed from the end of February to the first two weeks of March (O. Maestrini, pers. Com. 2011). This would fit with the low inter-individual variability observed in the $\delta^{18}O$ record.

4.2.3 Inter-group variability in the $\delta^{18}O$ values

When plotted together, combined $\delta^{18}O$ incisors sequences of domestic and feral pigs were out of phase (Fig.9), most likely due to the difference in the timing of birth between domestic and feral populations, born respectively in November and potentially from end of January to the end of April. However, a direct comparison of the $\delta^{18}O$ sequences measured in domestic and feral pig incisors was difficult due to a difference in the timing of tooth growth between both taxa. Indeed, feral pig incisors recorded half an annual cycle over approximately 30 mm, while domestic pig incisors recorded the same time sequence over 20 to 25 mm (estimations

based on the incisors combined sequences), highlighting a slower growth rate for the latter. This might also partly explained why the annual amplitude of variation of $\delta^{18}O$ values (estimated from incisors combined sequences) differed: 1.1 ‰ in domestic pigs and 2.9 ‰ in feral pigs, even though both populations live in similar environments and have access to the same types of water sources (streams). A slower rate of mineralization in domestic pig incisors would cause a higher dampening effect and therefore reduction of the amplitude of the isotopic signal.

4.3 Seasonal dietary behaviour from enamel $\delta^{13}C$ sequences

Both feral and domestic pig populations were raised in a C_3 environment with a baseline modal $\delta^{13}C$ value for plants close to -27 ‰ (Tieszen and Boutton, 1989). Warinner and Tuross (2009) calculated a +14.1 ‰ spacing between diet and bioapatite in pigs, which would lead to a baseline value of -12.9 ‰ in tooth enamel. It is notable that the $\delta^{13}C$ values measured in domestic pig enamel were normally higher than -12.9 ‰ (Fig.4), whereas the $\delta^{13}C$ values measured in feral pigs were almost consistently lower (Fig.5). Minimum $\delta^{13}C$ values in the feral pig canines were on average impoverished by 1.4 ‰ relative to domestic pigs. This impoverishment might reflect a difference in behaviour – these feral pigs perhaps preferentially lived under a denser tree cover – or a difference in metabolism, which lead to a difference in the diet-bioapatite spacing.

The pellets included in the domestic pig diet, with a mean value of -27.2 ‰, would not specifically affect the $\delta^{13}C$ values of enamel bioapatite. However, the C_4 component (maize), could raise the $\delta^{13}C$ values measured in bioapatite to up to +3.8 ‰, estimated from the modal C_4 plant $\delta^{13}C$ value and a +1.5 ‰ spacing between maize leaf and kernel (Hobbie and Werner, 2004), and a mean isotope enrichment (ε^*) value between diet and pig enamel of +14.5 ‰ (calculated from the data from Warinner and Tuross, 2009). However, the exact proportion in the domestic pigs diet was unknown. Regular consumption of maize over the year by domestic pigs might explain the overall shift in the $\delta^{13}C$ values measured in the domestic population compared to those measured in wild boars. Domestic pig canines are also characterized by a great inter-variability in the $\delta^{13}C$ maxima, ranging from -10.6 ‰ (PCR4) to -5.4 ‰ (PCR5). This difference may be ascribed to food preferences and difference in the proportion of maize included in the diet. Such $\delta^{13}C$ values would correspond respectively to ~3 % and 35 - 40 % of maize in the diet. Those are minimum estimations, because of the possible dampening of $\delta^{13}C$ values caused by the duration of enamel mineralization. In the latest formed part of the canine, $\delta^{13}C$ values decreased to a typical value for a pure C_3 plant diet in domestic pigs. This might reflect the ceasing of maize consumption over the last winter before slaughter, as recommended by Corsican herding practices for reasons directly linked to the purpose of meat transformation.

Other food items seasonally available to both feral and domestic pig populations include acorns from autumn to early spring, and fruits, roots, or food gathered in aquatic ecosystems in the summer. All have higher $\delta^{13}C$ values than C_3 plants leaves. An acorn seed diet, with a mean value of $\delta^{13}C$ = -25.5 ‰, would raise $\delta^{13}C$ values towards -11.4 ‰ in enamel. Fruits and roots are ^{13}C-enriched by up to 3 ‰ compared to leaves (Cernusak et al., 2009). Therefore the seasonally higher $\delta^{13}C$ values recorded in the summer (SC4C) or in the winter (SC1C) in feral pig canines (Fig.5) could reflect consumption of such items.

In the domestic pig canines, a peak in $\delta^{13}C$ values was located at the end of the second winter or beginning of the second spring (Fig.4). In PCR5 canine, another peak is situated at the end of the first summer. These two periods correspond to food shortage times, during

which pigs may have difficulties finding enough food in the natural environment. Those peaks, which raised to as high $\delta^{13}C$ values as -6 ‰, are likely to include a C_4 component in the diet. They may therefore correspond to an increased consumption of maize.

Conclusion

Among all the sampled teeth (I1, I2, C, M1 and M2), the combination of the two first incisors is likely to provide the most accurate data for the study of birth seasonality. As a result, the $\delta^{18}O$ sequences published in this paper provide a reference data set for grouped domestic pigs births around mid-autumn and feral pigs births towards the end of winter.

The male canine is the only tooth that provides an easily readable isotopic record over a whole year or more. The 26 month-old pigs of our dataset provided a year and a half record.

The oxygen stable isotope record observed in these teeth fits within the timing for tooth formation given in the literature, with a slight delay suggesting a later mineralization process. The duration could not be assessed precisely, but was shortest in male canines.

The $\delta^{13}C$ values measured from these feral pigs constitute the first isotopic reference data set for a wild population living in a Mediterranean environment. The isotopic record in the canine enamel enables the observation of short seasonal variations in the isotopic composition of the diet, linked to the seasonal occurrence of food resources like acorns, chestnuts and beechnuts from autumn to winter, and fruits, roots and resources from aquatic ecosystems in summer. In the domestic pigs, this record also allowed the detection of maize in the food supply during the times of food shortage.

Applied to archaeological faunas, the joint analysis of incisors and canines will enable the qualification of the seasonal rhythm of pig herding practices in more concrete terms. Indeed, information on the seasonality of births should also allow for precise interpretation of the mortality profiles in terms of slaughtering seasonality, as it is linked to the modalities of pork production. However, slaughtering also depends on the seasonal variation of the availability of food resources, for which a precise interpretation could be constructed from the canine record.

Acknowledgements

This work was financially supported by the CNRS and Région Ile-de-France for stable isotope mass spectrometry. A doctoral fellowship to D. Frémondeau and funds for stable isotope analysis were provided by a European Research Council Starting Grant (SIANHE Starting Grant n°202881 dir. M. Balasse). The stable isotope analyses were performed at the Service de Spectrométrie de Masse Isotopique du Muséum national d'Histoire naturelle (SSMIM) in Paris. We would like to thank Antoine Cucchi who provided the domestic pig mandibles as well as information on herding practices. Thanks are due to Oscar Maestrini of INRA Lab of Corte for providing wild pig mandibles and information about seasonal reproductive behaviour. Many thanks to Eric Pellé of the Service de Préparation Ostéologique et Taxidermique (SPOT) of the Muséum national d'Histoire naturelle in Paris, for the osteological preparation of all the mandibles. We are also thankful to the two anonymous reviewers for their comments, which contributed to improve this manuscript, as well as to Ardern Hulmebeaman who kindly accepted to revise the quality of the English.

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Table 1: The wild boar reference set.

Code 1	Code 2	Sex	Estimated Age	Region of Capture
CO-WB-CA-02	SC1	♀	3-4 y	Bocca di Pigna
CO-WB-CA-01	SC2	♂	≈ 2 y	Bocca di Pigna
CO-WB-TRA-01	SC3	♂	≈ 2 y	Tralonca
CO-WB-SOL-01	SC4	♂	≥ 3 y	Solenzara

Table 2: Carbon contents and $\delta^{13}C$ measured from acorns and pellets samples.

Sample	n	%C	δ13C (‰)		
			Min	Max	Mean
acorn + cup	5	45.6	-27.2	-26.2	-26.7
cup	5	48.6	-27.4	-25.5	-26.7
acorn pericarp	5	47.4	-27.1	-25.4	-26.3
acorn seed	5	44.2	-25.9	-25.2	-25.5
pellets	5	41.6	-27.5	-26.7	-27.2

Table 3: Amplitude of variation of the stable oxygen and carbon isotope ratios measured from enamel bioapatite of domestic pigs. Values are expressed versus VPDB standards (‰).

	Domestic pigs $\Delta^{13}C_{max\text{-}min}$ (‰)			**Domestic pigs $\Delta^{18}O_{max\text{-}min}$ (‰)**		
	Min	**Max**	**Mean**	**Min**	**Max**	**Mean**
I1	1.3	4.2	2.3	0.4	0.9	0.7
I2	1.5	3.3	2.2	0.8	1.8	1.4
C	2.8	7.7	5.3	1.4	2.4	1.9
M2	0.3	1.6	1.0	0.3	1.2	0.8
M3	0.9	3.0	1.8	0.6	1.2	0.9

Table 4: Amplitude of variation of the stable oxygen and carbon isotope ratios measured from enamel bioapatite of wild pigs. Values are expressed versus VPDB standards (‰).

	Wild pigs $\Delta^{13}C_{max-min}$ (‰)			Wild pigs $\Delta^{18}O$max-min (‰)		
	Min	**Max**	**Mean**	**Min**	**Max**	**Mean**
I1	1.0	1.8	1.4	0.8	1.9	1.3
I2	1.0	3.2	1.7	1.0	2.5	1.8
C	1.2	2.5	1.9	1.9	3.7	2.8
M2	0.3	1.4	1.0	0.3	1.6	0.9
M3	0.7	2.5	1.4	1.2	1.3	1.2

Figure 1: Provenience of the domestic and wild pigs: Radicci (open symbol) Bocca di Pigna (1), Solenzara (2) and Tralonca (3).

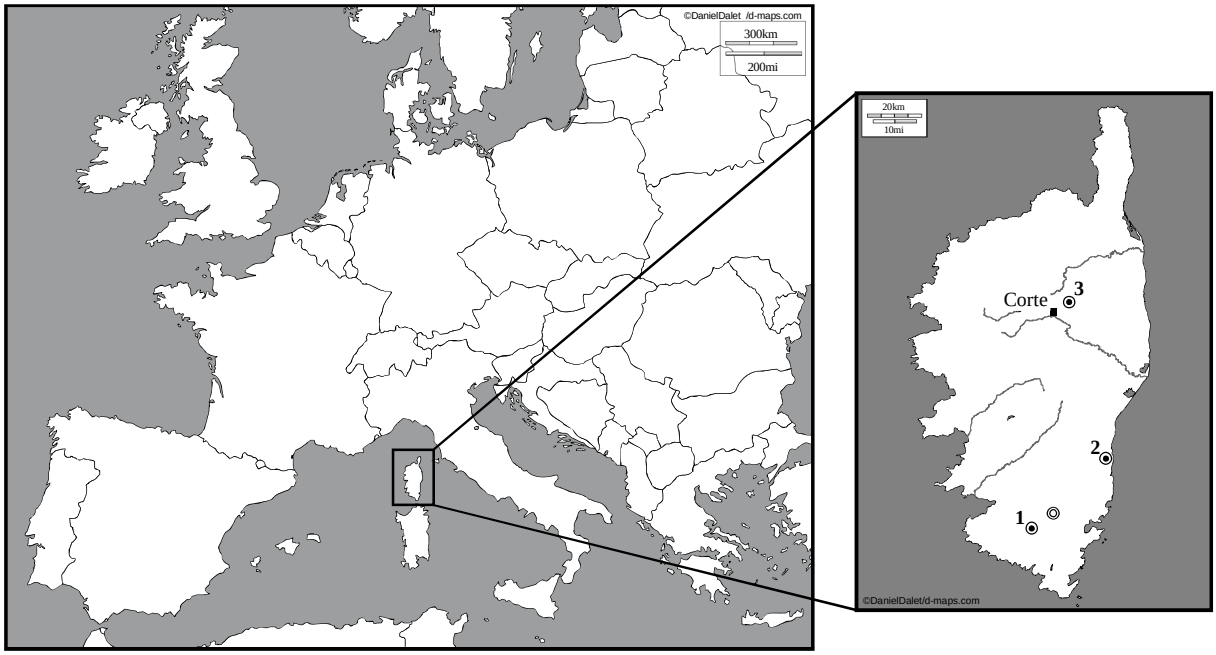

Figure 2: Timing of crown growth in *Suidae* (after McCance et al., 1961; Tonge and McCance, 1965; Hayashi et al., 1977; Bull and Payne, 1982; Magnell, 2002; Carter and Magnell, 2007). Dotted lines for crown formation represent the variability in literature data. Below each line are reported the $\delta^{18}O$ sequences recorded in each kind of tooth of the Radicci domestic pigs.

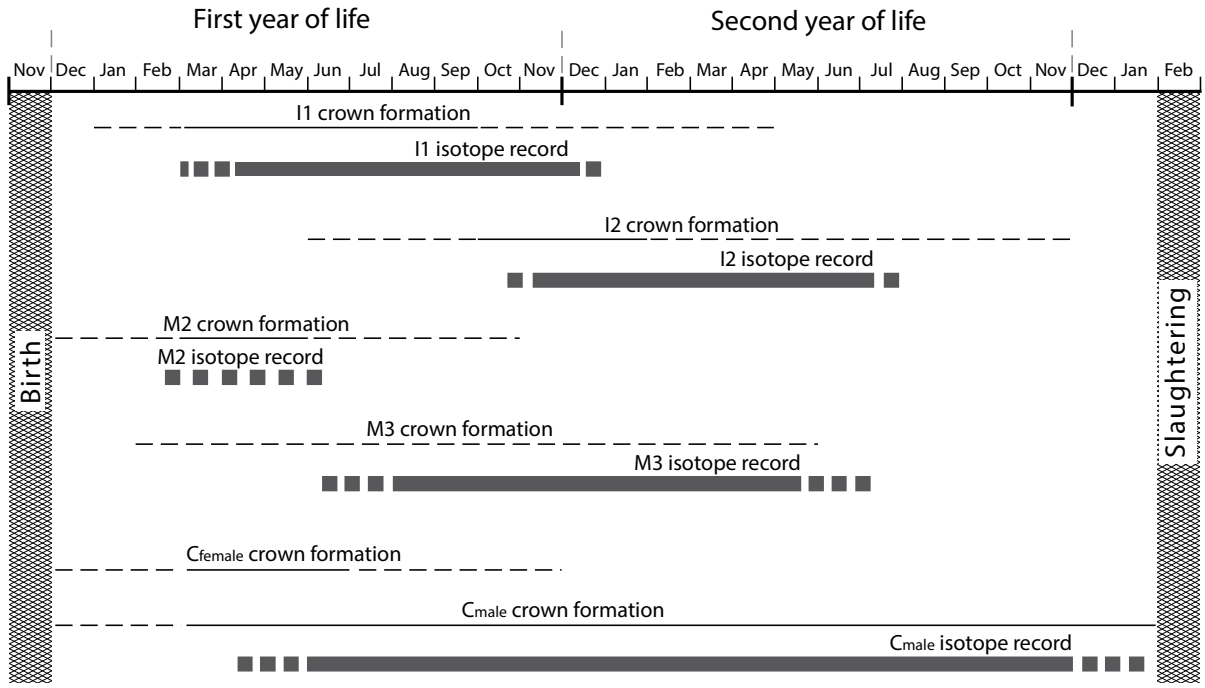

Figure 3: Sampling of enamel on the lower incisors (a: I1; b: I2), canine (c) or molars (d: M2; e: M3). (scale = 1 cm).

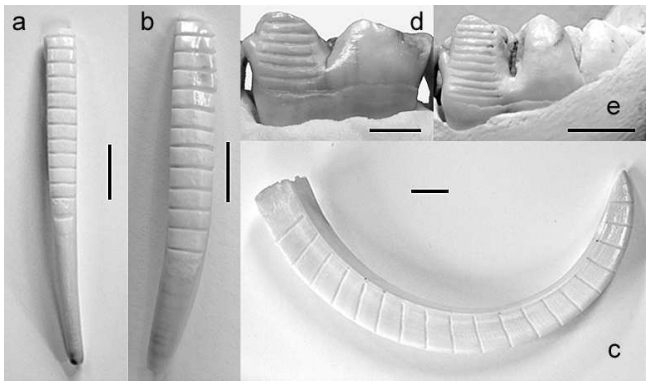

Figure 4: Intra-tooth variation of carbon ($\delta^{13}C$ – solid circles) and oxygen ($\delta^{18}O$ – open circles) isotope ratios of enamel bioapatite of the domestic pigs from Radicci. On each graph, the left axis refers to $\delta^{18}O$ and the right to $\delta^{13}C$.

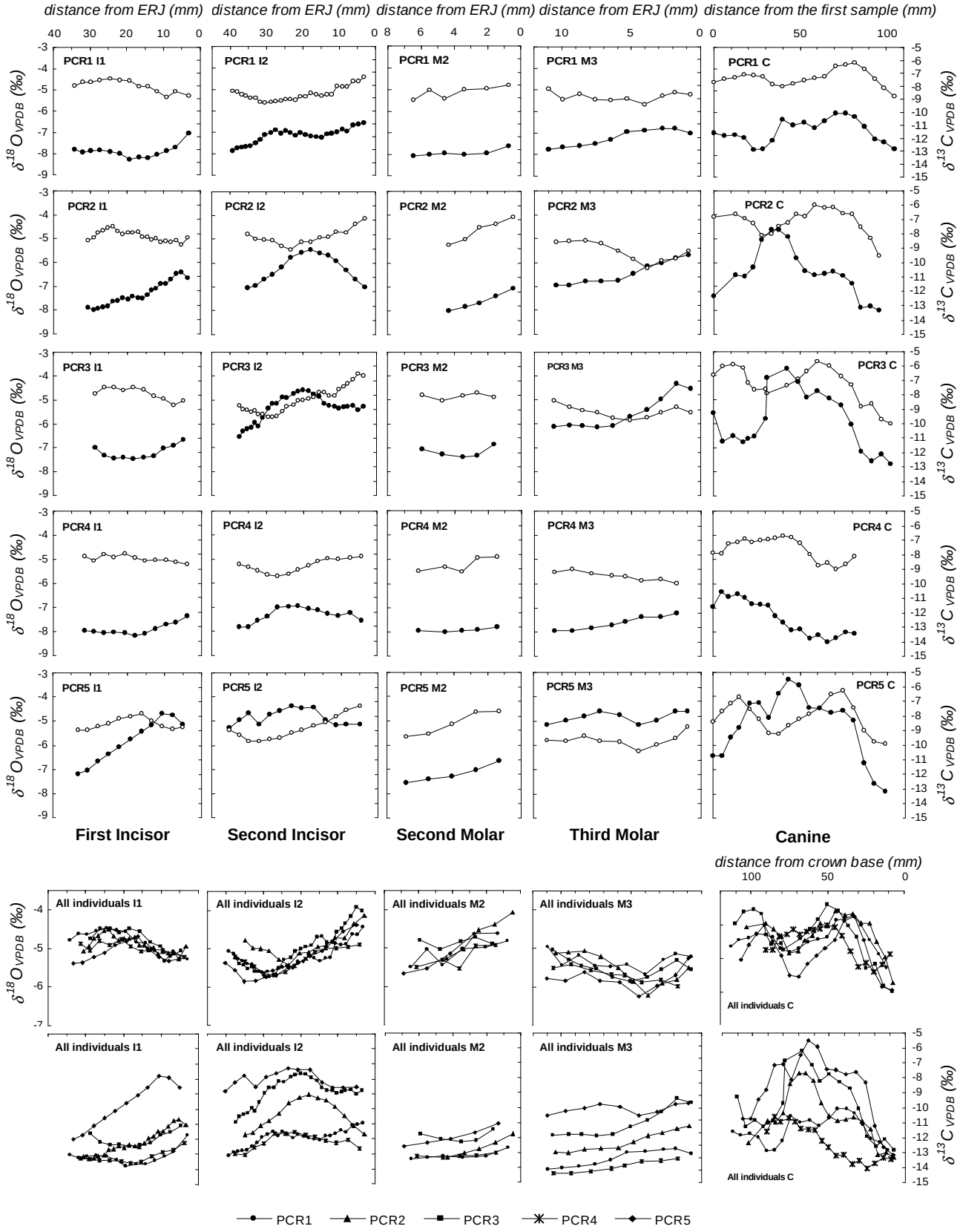

Figure 5: Intra-tooth variation of carbon ($\delta^{13}C$ – solid circles) and oxygen ($\delta^{18}O$ – open circles) isotope ratios of enamel bioapatite of the wild pigs. On each graph, the left axis refers to $\delta^{18}O$ and the right to $\delta^{13}C$.

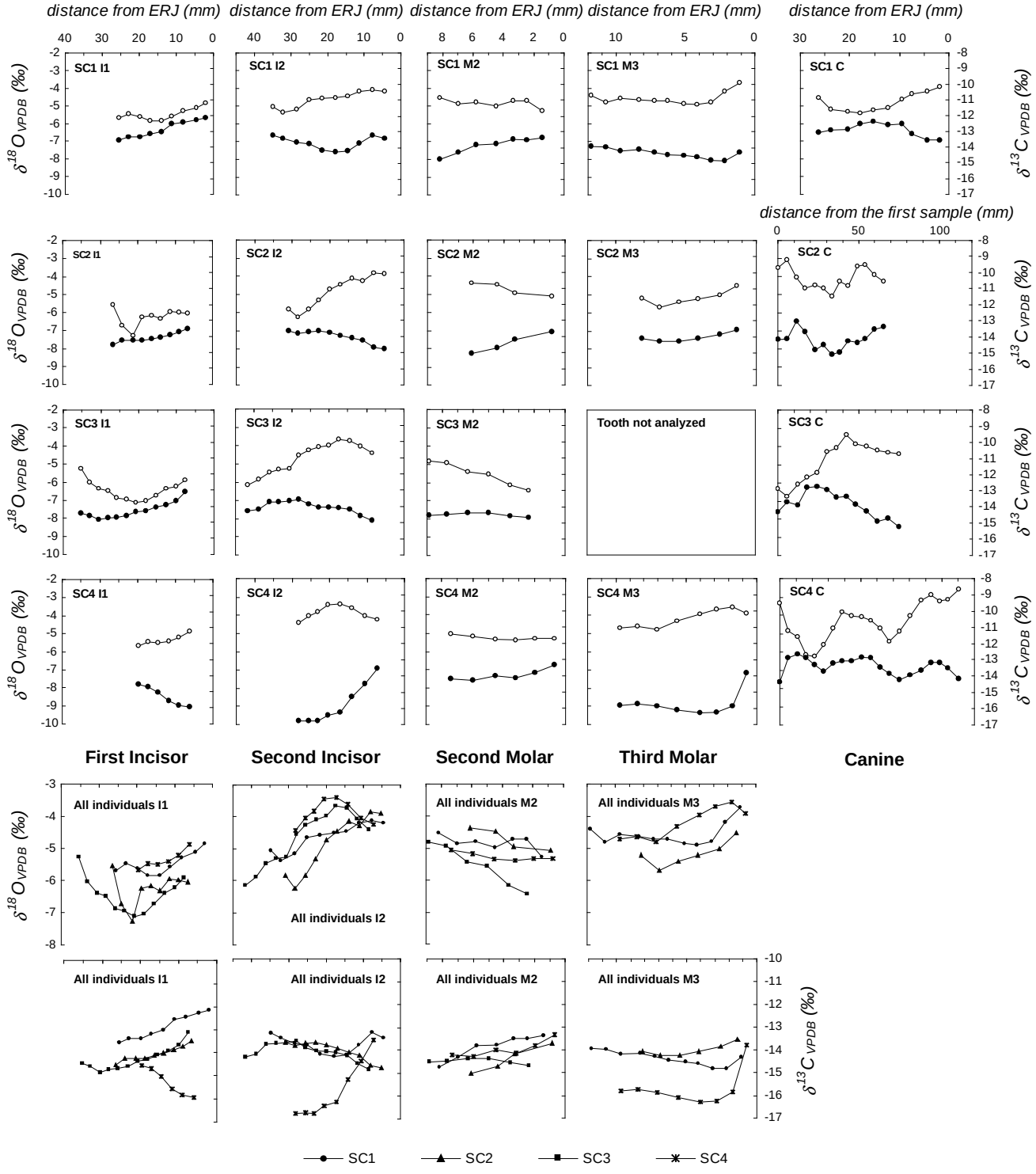

Figure 6: Combined $\delta^{18}O$ (a) and $\delta^{13}C$ (b) sequences of I1 and I2 of the domestic pigs of Radicci (I1: grey curves; I2: black curves).

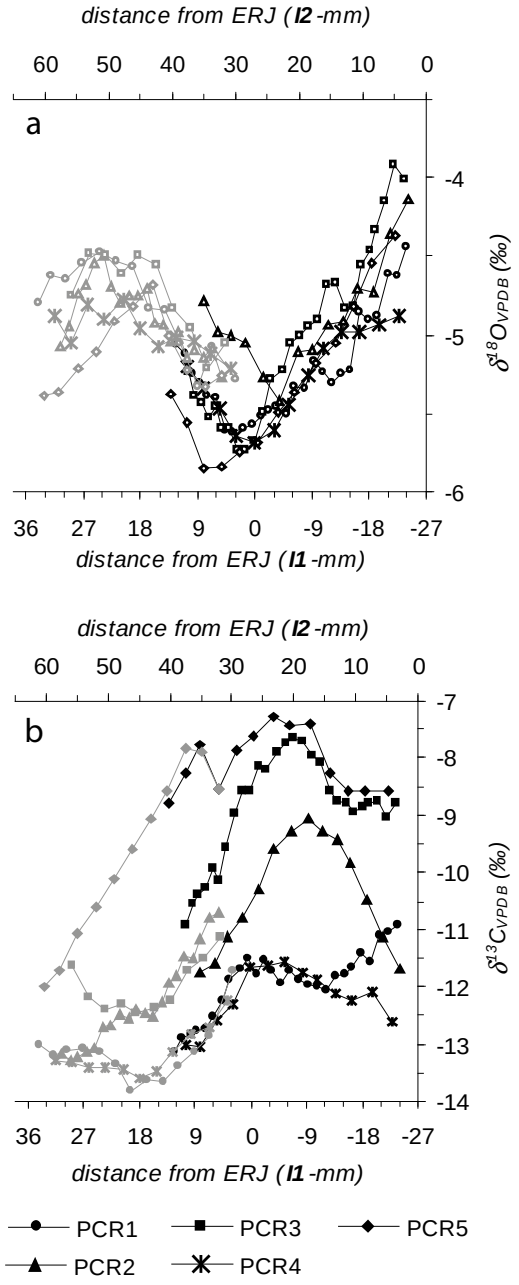

Figure 7: Combined $\delta^{18}O$ (a) and $\delta^{13}C$ (b) sequences of I1 and I2 of the wild pigs (I1: grey curves; I2: black curves).

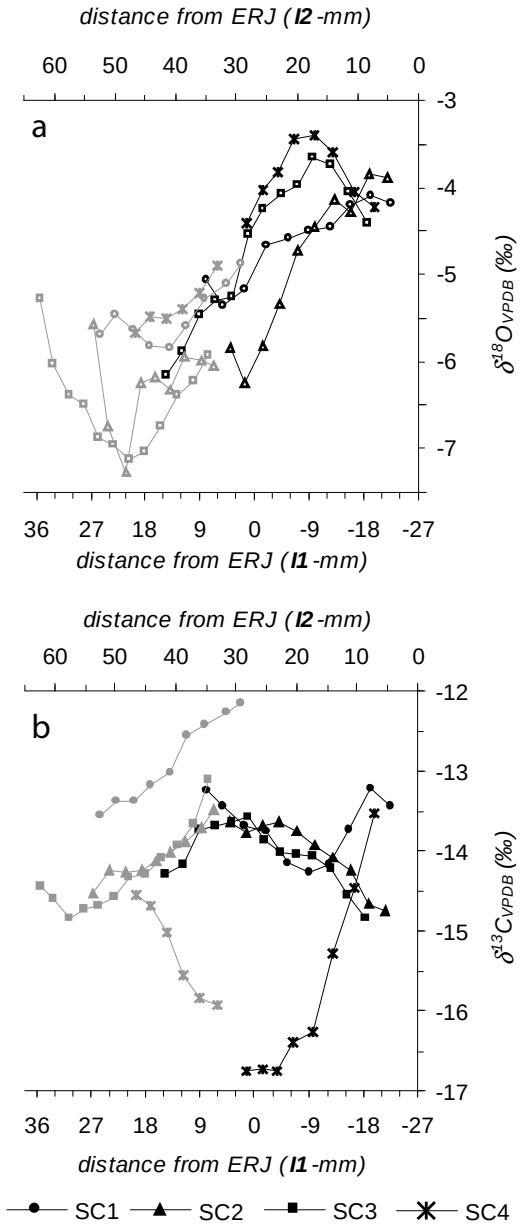

Figure 8: $\delta^{18}O$ (open symbols) and $\delta^{13}C$ (solid symbols) sequences recorded in I2 crowns after normalisation of the distance from ERJ.

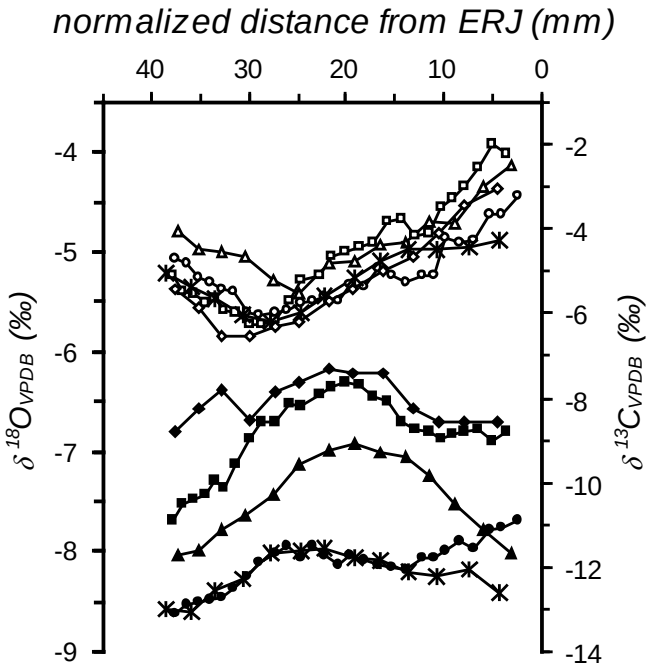

Figure 9: Incisors (I1 + I2) combined $\delta^{18}O$ sequences of the domestic (grey curves) and wild pigs (black curves).